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THE HEAT RESISTANCE OF INTERTIDAL SNAILS AT SHIRAHAMA, WAKAYAMA-KEN, JAPAN[1)]

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It is well known that animals differ greatly in their tolerance of extreme temperatures, high or low, and that such differences are correlated with the temperatures of the organism's natural environment. With regard to a particular ecological group, the intertidal animals, it has been frequently stated that they are subjected to and adapted to tolerate much higher temperatures than related forms which are permanently submerged, and that within a particular area the resistance of a particular species is correlated with its position in the intertidal zone.

Intertidal organisms live an amphibious life, being periodically in or out of the water. Since the amplitude of temperature changes in air greatly exceeds those in water, one would expect that one of the adaptations of a marine organism to periodic existence out of the water would be the ability to stand high temperatures. The magnitude of temperatures to be tolerated would then also depend on the climatic characteristics of a particular area. While these principles have often been stated in recent reviews (GUNTER 1957, NEWELL 1964, USHAKOV 1964), and their verity can hardly be doubted, underlying evidence is often sketchy, incomplete, or based on faulty experimentation. Most of the relevant data apply to relatively temperate zones, and are based on criteria which, as will be explained in the section on methods, are only useful in a comparative sense.

In the voluminous recent Russian literature on this subject (see the comprehensive reviews by ALEXANDROV 1964, USHAKOV 1964, and the collection of articles, Problems of Cytology, 1961) the adaptation of an organism to the temperature of its surrounding has been taken largely for granted, at least in all the work concerning intertidal molluscs, and the inquiry deals with the heat resistance of *isolated* muscles and enzymes. Some of this work, insofar as it is relevant to the present investigation, will be discussed later. While there now exists massive evidence for a correlation of muscular activity and enzyme action according to the temperatures to which intertidal molluscs in different climates and tidal zones are subjected, there still exists a gap in our knowledge concerning the tolerance of the *whole* organism to high temperatures. I began the analysis of the heat resistance of intertidal snails with what I considered

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more valid methods several years ago with *Littorina littorea* at Woods Hole (FRAENKEL, 1960) and *Littorina neritoides* in the Mediterranean (FRAENKEL, 1961). A stay of several weeks at the Seto Marine Biological Laboratory during August 1963 gave me a welcome opportunity to extend these studies to the very rich intertidal prosobranchean fauna of a relatively warm region in southwestern Japan.

Methods

I previously pointed out (1960, 1961) that most of the existing data on the tolerance of high temperatures by marine invertebrates are unreliable, and of use only in a comparative sense. This specifically applies to a string of papers on intertidal molluscs (HUNTSMAN & SPARKS 1924, HAYSE 1929, HENDERSON 1929, BROEKHUYSEN 1940, EVANS 1948, SOUTHWARD 1958), all applying a method devised by HUNTSMAN & SPARKS. The animals were heated in sea water at a temperature increase of 1°/5 minutes, and were removed after they showed signs of heat coma. The highest temperature which they could survive was determined by allowing them to recover in colder water for 1 hour, and then looking for a response to prodding with a pin. These investigations gave a fairly good correlation between lethal temperature and position in the intertidal zone, especially in BROEKHUYSEN's (1940) data from False Bay, Cape Province, South Africa (see the comprehensive tabulation in GUNTER 1957). However, they cannot be construed as absolute temperature values of heat resistance, since the animals were subjected to rising temperatures, and for only a very short period at each temperature. These shortcomings were eliminated by the method first proposed by me in 1960, and used in 1961 and the present paper. This consisted of heating the snails at constant temperatures for one hour. As a criterion for survival I used a behavioral response, the resumption of normal locomotion which in the majority of cases included crawling up the sides of the container and out of the water. This constitutes a more realistic measure of resistance, since reactions to prodding still occur after exposure to temperatures which invariably result in the death of the snail. As the previous (1960, 1961) and present results show, "full" recovery is often delayed and requires a recovery period of one day or more. This makes any method which allows only a short recovery period, or none at all, subject to a great error. It is obvious that coordinated crawling cannot be an entirely valid criterion for full recovery, since the snails may conceivably die later. Any more elaborate measure of recovery would however have been very unrealistic and time consuming.

All the snails used in the present study were collected at low tide from the rocks and beaches surrounding the peninsula on which the Seto Laboratory stands, and were used shortly after collecting. The taxonomic nomenclature is that in the book by HABE (1961) and the New Illustrated Encyclopedia of the Fauna of Japan (1965).

Table 1. The resistance of the prosobranchean snail *Nodilittorina pyramidalis* (QUOY et GAIMARD) to high temperatures, after exposure for one or two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering
August 9, 1963	46–46.5°	60	20	17
		120	20	14
August 9, 1963	48–48.5°	60	10	10
		120	10	10
August 13, 1963	49°	30	12	12
		60	10	0

Table 2. The resistance of the prosobranchean snail *Nodilittorina granularis* (GRAY) to high temperatures, after exposure for one or two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering	Remarks
August 12, 1963	46.2°	60	10	10	
		120	10	7	
August 9, 1963	46–46.5°	60	10	10	
		120	10	10	
August 11, 1963	47.2°	60	10	5	
		120	10	5	
August 10, 1963	48–48.5°	60	10	3	after 1 day: 6 dead, 1 alive
		120	10	1	
August 13, 1963	49°	60	10	0	

Table 3. The resistance of the prosobranchean snail *Planaxis sulcatus* (BORN) to high temperatures, after exposure for one to two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering	Remarks
August 9, 1963	46–46.5°	60	10	10	
August 11, 1963	47.2°	60	10	8	
		120	10	10	
August 10, 1963	48–48.5°	60	10	9	
		120	10	1	after 1 day: 9 inactive but reactive
					after 2 days: dead
August 13, 1963	49°	60	10	0	

Table 4. The resistance of the prosobranchean snail *Littorina brevicula* (PHILIPPI) to high temperatures, after exposure for one or two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering	Remarks
August 15, 1963	43.2°	120	10	9	
August 16, 1963	44.1°	60	10	8	
		120	10	10	of these 8 recovered the following day
August 17, 1963	45.1°	60	10	7	of these 5 recovered by next morning, 3 more remained reactive for several days
		120	12	8	3 recovered by next morning
August 18, 1963	46°	60	20	10	10 dead following day
		120	20	8	12 reactive, but died later
					8 recovered by next morning
August 12, 1963	46.3°	60	10	1	
		120	10	1	
August 11, 1963	47.2°	60	10	6	recoverd by next morning
		120	10	2	
August 19, 1963	47.2°	60	20	0	reactive after treatment
		120	20	0	
August 10, 1963	48–48.5°	60	20	0	2 slightly reactive following day after 2 days: all dead

Table 5. The resistance of the prosobranchean snail *Peasiella roepstorffiana* (NEVILL) to high temperatures, after exposure for one or two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering	Remarks
August 15, 1963	43.3°	60	25	25	recovered very quickly
August 16, 1963	44.1°	60	15	15	recovered very quickly
		120	10	10	recovered very quickly
August 17, 1963	45.1°	60	16	12	8 recovered same day, 4 next morning
		120	16	15	6 recovered same day, 9 next morning
August 18, 1963	46°	60	17	17	
		120	20	12	
August 12, 1963	46.2°	60	10	8	recovered immediately
		120	20	17	4 recovered immediately, 13 by next morning
August 19, 1963	47.2 °	60	20	15	11 recovered by next morning
		120	20	4	all reactive after treatment
August 21, 1963	48°	60	25	1	

Table 6. The resistance of the prosobranchean snail *Heminerita japonica* (DUNKER) to high temperatures, after exposure for one or two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering	
August 17, 1963	45.1°	60	10	9	
August 18, 1963	46.0°	60	10	10	
August 12, 1963	46.2°	30	10	3	
August 19, 1963	47.2°	60	10	1	

Table 7. The resistance of the prosobranchean snail *Theliostyla albicilla* (L.) to high temperatures, after exposure for one or two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering	Remarks
August 14, 1963	42.3°	60	10	9	
		120	10	8	
August 15, 1963	43.3°	60	10	9	
		120	10	9	
August 16, 1963	44.1°	60	10	7	
		120	10	4	
August 17, 1963	45.1°	60	10	1	reactive after treatment
		120	10	0	reactive after treatment
August 9, 1963	46.3°	60	10	0	after 2 days: inactive, slightly reactive
August 12, 1963	46.2°	30	10	0	after 2 days: 7 dead, 3 bearly reactive

Table 8. The resistance of the prosobranchean snail *Lunella coronata coreensis* (RECLUZ) to high temperatures after exposure for one or two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering	Remarks
August 20, 1963	40.4°	60	5	5	
August 14, 1963	42.3°	60	10	10	recovery within several hours
		120	10	8	
August 15, 1963	43.3°	60	10	4	recovery by following morning

Table 9. The resistance of the prosobranchean snail *Morulina granulata* (DUCLOS) to high temperatures, after exposure for one or two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering	Remarks
August 15, 1963	42.3°	60	10	3	
August 15, 1963	43.3°	60	10	0	9 reactive after treatment, but did not recover
		120	5	2	2 recovered by next morning

Table 10. The resistance of the prosobranchean snail *Thais clavigera* (KÜSTER) to high temperatures, after exposure for one or two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering	Remarks
August 14, 1963	42.3°	60	10	8	
		120	10	0	
August 15, 1963	43.3°	60	10	1	
		120	10	2	alive after treatment, 2 recovered by next morning, 8 dead on 2nd day

Table 11. The resistance of the prosobranchean snail *Monodonta labio* (L.) to high temperatures, after exposure for one or two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering	Remarks
August 20, 1963	40.4°	60	5	5	
August 20, 1963	42.2°	60	5	5	
August 20, 1963	43.4°	60	5	0	
August 16, 1963	44.1°	60	10	0	reactive after treatment

Table 12, The resistance of the prosobranchean snail *Chlorostoma argyrostoma lischkei* (Tapparone-Canefri) to high temperatures, after exposure for one or two hours, at Shirahama.

Date	Temperature	Exposure period minutes	Number in experiment	Number recovering	
August 22, 1963	38.5°	60	5	3	
August 20, 1963	40.4°	60	5	0	
August 14, 1963	42.3°	60	10	0	

Results

The results of the experiments are given in tables 1–12.

1. *Nodilittorina pyramidalis* (QUOY et GAIMARD). This snail occurs high in the intertidal zone, and higher up in the spray zone facing the open water. (Table 1)

2. *Nodilittorina granularis* (GRAY). Occurs in the same locations in the upper intertidal zone as *N. pyramidalis*. It is especially numerous on the stones of the breakwater in front of the laboratory. (Table 2)

3. *Planaxis sulcatus* (BORN). Occurs in the upper intertidal zone. (Table 3)

4. *Littorina brevicula* (PHILIPPI). Occurs in the upper intertidal zone. (Table 4)

5. *Peasiella roepstorffiana* (NEVILL). Occurs in shallow tide pools in the upper intertidal zone. (Table 5)

6. *Heminerita japonica* (DUNKER). Occurs on the rocky plateau in the middle reaches of the intertidal zone in front of the laboratory. (Table 6)

7. *Theliostyla albicilla* (L.). Occurs in the middle intertidal zone in locations similar to those of *H. japonica*. (Table 7)

8. *Lunella coronata coreensis* (RECLUZ). Occurs in the lower intertidal zone which is dry for only short periods in the day. (Table 8)

9. *Morulina granulata* (DUCLOS). Occurs in the lower intertidal zone in shadowy and sheltered places. (Table 9)

10. *Thais clavigera* (KÜSTER). Occurs in the lower intertidal zone in shadowy and sheltered places. (Table 10)

11. *Monodonta labio* (L.). Is found in the middle to lower part of the intertidal zone, but always under stones when it is not covered by water. (Table 11)

12. *Chlorostoma argyrostoma lischkei* (TAPPARONE-CANEFRI). Occurs in the lowest intertidal zone at the water's edge, most abundantly under stones in the water. (Table 12)

Discussion

The results of the heating experiments are summarized in table 13, and arranged in order of decreasing resistance. The temperatures shown are those which reflect best the combined data obtained with each species, the highest temperature which, after one hour of exposure, permitted one half or more of the snails to recover to the extent of resuming normal locomotion and crawling up to the water's edge or out of the water. The results show at a glance a striking correlation of heat resistance with the position in the tidal zone. The highest resistance, 47 to 48°, is exhibited by *Nodilittorina pyramidalis, Nodilittorina granularis, Planaxis sulcatus* and *Littorina brevicula* which inhabit the upper part of the intertidal zone and the spray zone above, and which are out of the water most of the time.

Interestingly, most of these species are Littorinidae, a family whose numerous species are the most typical inhabitants of the upper reaches of intertidal zones all over the world. Of similar resistance is another Littorinidae, the tiny *Peasiella roepstorffiana* which lives in shallow splash pools in the upper and middle intertidal region where the water may warm up considerably by insulation. Not being subjected to ordinary wave action, they often find themselves entirely out of the water for long periods. Furthermore, their minute size (1 mm across) would favor a rapid heating up.

In the next category of resistance are two species of Neritidae, *Heminerita japonica* and *Theliostyla albicilla* which inhabit the middle part of the tidal zone and can resist 46° and 44° respectively. Neritidae is another family of prosobranchean snails whose members typically inhabit tidal zones.

The third category shows still lower resistance and consists of five species which inhabit sheltered or shadowy places in the lower reaches of tidal zones. They are

Table 13. The heat resistance of intertidal snails of Shirahama, Japan. The highest temperatures are given from which the snails can recover after one-hour exposure. Experiments performed during August 1963.

Name	Family	Temperature	Occurrence
Nodilittorina pyramidalis	Littorinidae	48.5°	spray zone
Nodilittorina granularis	Littorinidae	47°	spray zone
Planaxis sulcatus	Planaxidae	48°	upper part of intertidal zone
Littorina brevicula	Littorinidae	47°	upper part of intertidal zone
Peasiella roepstorffiana	Littorinidae	47°	shallow splash pools
Heminerita japonica	Neritidae	46°	middle part of intertidal zone
Theliostyla albicilla	Neritidae	44°	middle part of intertidal zone
Lunella coronata	Turbinidae	43°	lower part of intertidal zone in sheltered or shadowy places or under stones
Morulina granulata	Muricidae	42°	lower part of intertidal zone in sheltered or shadowy places or under stones
Thais clavigera	Muricidae	42°	lower part of intertidal zone in sheltered or shadowy places or under stones
Monodonta labio	Trochidae	42°	lower part of intertidal zone in sheltered or shadowy places or under stones
Chlorostoma argyrostoma lischkei	Trochidae	39°	lower part of intertidal zone at the water's edge

practically always in reach of waves, and the environment never dries up entirely. Four of these species, *Morulina granulata, Thais clavigera, Monodonta labio* and *Lunella coronata coreensis* resisted temperatures of about 42°. The first two mentioned belong to the family Muricidae whose members typically occur in shallow water up into the lower tidal zones. The snail with the lowest resistance in this table (39°), *Chlorostoma argyrostoma lischkei,* is in the Trochidae, top shells, a family whose members are often found at the water's edge.

The temperature resisted by the most resistant forms are surprisingly high by comparison with figures published by other authors, exceeding even the 46–47° value reported for the mediterranean Littorinid, *L. neritoides,* which inhabits rocks far above the water line and is subjected to spray only in stormy weather (FRAENKEL 1961). For *Littorina littorea,* an inhabitant of much cooler regions, the comparable figure was 40 to 41° (FRAENKEL 1960). However, still higher temperatures of resistance (up to 50°) were obtained for several Littorinidae in the Carribean area, as will be mentioned later (FRAENKEL 1966).

This is the place to compare our results with corresponding data obtained on some of the same species by OHSAWA and TSUKUDA (1956) and OHSAWA (1956). These authors investigated at length the heat tolerance and acclimation of *Nodilittorina granularis* from the same locations at Shirahama and also obtained some additional data from related periwinkles. This discussion will be largely limited to aspects of their work which are comparable in aim and technique to my own. The criterion of a heat effect was the "extruding response" shown when a snail that had been kept out of the water in a closed state is returned to sea water. It is not obvious whether or to what extent the best extruding performance ("A") can be assumed as being equivalent to my criterion of "full" recovery. The snails were submitted for

periods of up to 4 hours to temperatures of 40°, 45° and 50°, while in dry air, NaCl solution isotonic to sea water, or distilled water. Of those kept at 50°, none immediately exhibited the response type A, but after a recovery period of 24 hours in air 50% of those that had been heat treated in NaCl solution for one hour exhibited type A response. This is 3 degrees higher than the 47° tolerated by our snails for 1 hour, a difference obviously due to differences in the criteria of recovery used. A comparison of the heat resistance of *Nodilittorina granularis* with that of two related species is not strictly possible with my own data because heating was performed in dry air which has less drastic consequences than heating in sea water. *Nodilittorina pyramidalis* was very slightly, and probably insignificantly, less resistant than *N. granularis*, while 70% of the *L. brevicula* recovered after exposure to 50° for 30 minutes, but only 10% after exposure for one hour. By our criteria *Nodilittorina pyramidalis* was the most resistant (48.5°), and the two other species were only slightly less (47°) resistant.

It would have been interesting to compare the results of the present study with the extensive results of DZHAMUSOVA (1962) on intertidal snails from diverse ecological locations in the arctic Atlantic and down the Siberian Pacific coast from near arctic conditions in the Sea of Okhotsk to almost subtropical conditions in the Sea of Japan, especially since these investigations include one of the snails investigated by me, *Littorina brevicula*, from the Japanese Sea. Unfortunately DZHAMUSOVA's investigation is entirely limited to a study of the heat resistance of *excised* muscles subjected to constant temperatures. At intervals the muscles were removed from the water bath, tested for contractility, and returned to the water bath if they still reacted. The possibility of recovery was not taken into consideration. Although the results show a striking correlation of resistance with the temperature of the natural surroundings and tidal zonation similar to that brought out in my own data, there is no possible basis of comparison of absolute temperature values. By DZHAMUSOVA's criteria the muscles of *L. brevicula* can stand 42° for 100 minutes, as against 46–47° for 60–120 minutes by our criterion of full recovery of the whole organism. DZHAMUSOVA's result of 34° for *Littrorina littorea* compares similarly with our result of 40° for the same species. A criterion more comparable with DZHAMUSOVA's, namely the temperature at which visible reactions can still be elicited after heating for one hour, gave maximum temperatures 2–3° higher than those obtained using the criteria of "full" recovery (43° for *Littorina littorea*, FRAENKEL 1966). These considerations make it clear that the method used by DZHAMUSOVA is liable to depress greatly the reactivity of muscles when subjected to high temperatures.

Finally, mention should be made of a recent comprehensive investigation of the heat resistance of intertidal snails at a subtropical location in the Carribean Sea (the Bahaman Island Bimini), using exactly the methods employed at Shirahama (FRAENKEL 1966). The results were strikingly similar, with even still higher temperature values for the most resistant species: 49–50° for Littorinidae in and above the

upper intertidal zone (*Tectarius muricatus, Echinius nodulosus, Nodilittorina tuberculata* and *Littorina ziczac*), 45–46° for Neritidae in the middle tidal zone (*N. peloronta, N. versicolor,* and *N. tesselata*); 43–44° for the tidal pool forms *L. mespillum, L. meleagris* and *Puperita pupae* (Neritinae), and 37–40° for inhabitants of the lowest intertidal zone, *Thais rustica, Leucozonia ocellata* and *Columbella mercatoria.*

Summary

The temperature resistance of 12 species of intertidal snails from the surroundings of Shirahama was determined. The method consisted of submitting the snails to constant temperatures while they were submerged in sea water, for one and two hours, and then determining the highest temperature from which they recovered. The criterion for recovery was resumption of normal locomotion and crawling out of the water. The degree of resistance was found to be closely correlated with the position of the snails in the intertidal zone. The highest resistance, 47 to 48.5° (1 hour exposure), was exhibited by Littorinidae and *Planaxis* which inhabit the highest zone: *Nodilittorina pyramidalis, Nodilittorina granularis, Planaxis sulcatus* and *Littorina brevicula,* and a similar resistance by *Peasiella roepstorffiana* which inhabits shallow tidal pools. The Neritidae *Heminerita japonica* and *Theliostyla albicilla,* inhabitants of a middle tidal zone, withstood 46 and 44°. Snails from a still lower region, *Lunella coronata, Morulina granulata, Thais clavigera* and *Monodonta labio,* withstood 42–43°, and the topshell *Chlorostoma argyrostoma lischkei* which lives at the waters edge, 39°. These results are discussed in relation to the work of OHSAWA and TSUKUDA with some of the same species, with that of Russian workers on the heat resistance of isolated muscles of intertidal snails, and with another investigation by the author on related snails in the Caribbean area.

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